

11.0 THE LOTKA-LESLIE MODEL

11.1 Introduction

The life table is a useful technique for studies of a stationary population or of a single cohort. Changing populations require the additional features provided by the Lotka-Leslie models which add age-specific reproductive rates (m_x) to the survivorship (l_x) entries from which the classical life table is developed. A further feature of the Lotka-Leslie approach is the calculation of a stable age structure (c_x).

The use of life tables in ecology became popular after the classic paper of Deevey (1947). Most of the illustrations for natural populations were unfortunately based on observed age structures or band returns with little assurance that the age data came from stationary populations or that survival rates were constant in the banding data. More recently it has become evident that these are risky assumptions. Burnham and Anderson (1979) and Anderson et al. (1981) discussed the problems and gave tests of the underlying assumptions for banding data. Tait and Bunnell (1980) noted that ages of animals found dead could be used with m_x data to estimate λ , and Van Sickle et al. (1987) have conducted further exploration of that approach. Although dependable survival rates cannot be extracted from age structure samples (if used alone) of non-stationary living populations, some useful information can be obtained from the "apparent" survival rate calculated from such populations (Eberhardt 1988).

Since fluctuations in population size caused by human influences on natural populations have become nearly ubiquitous, the classical life table has become largely an abstraction and laboratory tool. Practical purposes are now better served by the Lotka-Leslie model. However, "life tables" now appear in the literature that contain reproductive data as well as survival data, and are often the basis for calculation of a rate of change of a dynamic population. It may be worthwhile to denote these tables as "augmented" life tables to distinguish them from the classical life table, which contains only data on survivorship.

11.2 Discrete and continuous population growth

Many large mammal populations exhibit what Caughley (1977) termed a "birth-pulse" growth pattern. That is, reproduction takes place in a relatively short period each year. In between these pulses of growth, mortality takes its toll, and the population decreases. However, most textbooks treat growth as a continuous process and use an exponential curve to represent the growth pattern. I believe that a more realistic model is that of compound interest, with the compounding done annually through the birth-pulse. Fig. 11.1 shows the

two models as compared to the likely actual trend of a population.

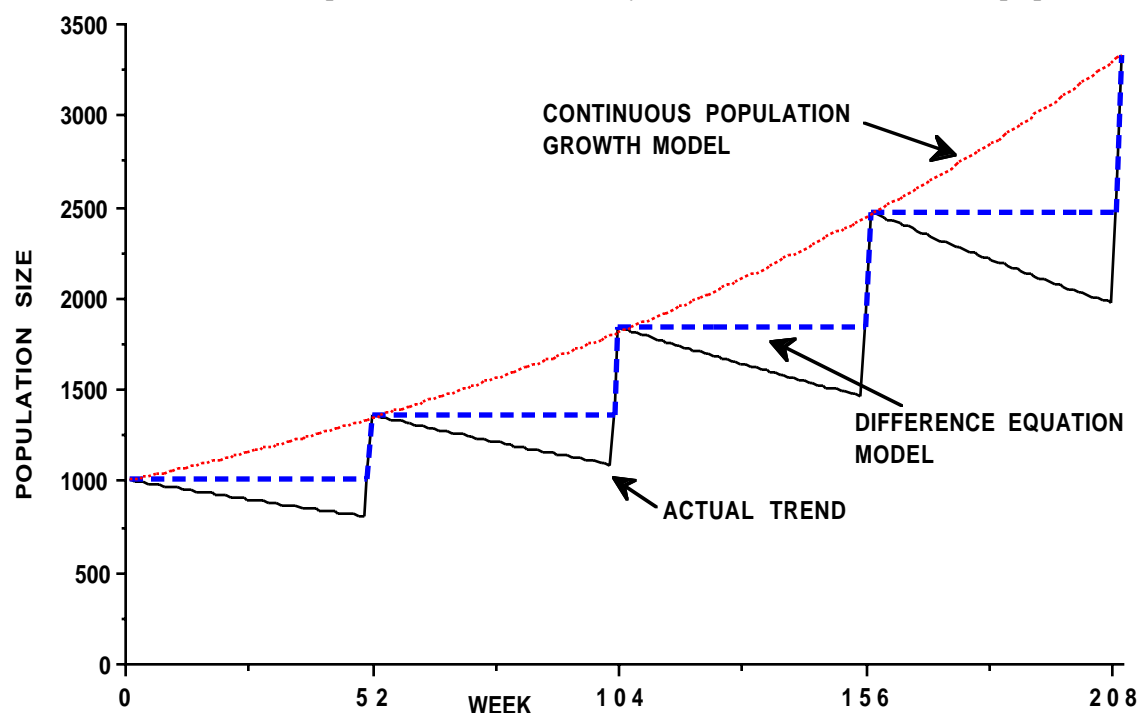


Fig. 11.1 Population growth modeled by continuous (exponential) and discrete (geometric) growth curves and the likely actual course of a population's size.

Very likely the best approach for most purposes is to use a "finite growth" model, using λ to denote the rate of change and writing:

$$N_t = N_0 \lambda^t \quad (11.1)$$

where N_0 denotes initial population size and N_t is population size t years later. We can then interpret λ as $\lambda = e^r$ for continuous growth and $\lambda = 1 + r$ for the compound-interest or geometric growth model. Fig. 1 suggests that the geometric growth model is closer to reality for birth-pulse populations, but the frequent use of the exponential model in texts makes it desirable to have the two interpretations in mind.

Another consideration is that we need methods to estimate rates of change, and using different methods can lead to some confusion. When there is a sequence of annual measurements of population size, the usual approach is that of log-linear regression. That is, we take the natural logarithm of population size and convert eq.(11.1) to:

$$\log_e N_t = \log_e N_0 + t \log_e \lambda \quad (11.2)$$

and fit a linear regression of the form $y = a + bx$. Then the slope (b) estimates $\log_e \lambda$, and if we use the interpretation in which $\lambda = e^r$, then $\hat{r} = b$ inasmuch as $\log_e e^r = r$. Using the interpretation in which $\lambda = 1 + r$, then b estimates $\log(1 + r)$, and we have to take the antilog and subtract unity to get r .

In some circumstances, however, we may want to estimate rate of change from two successive measurements of population size, getting:

$$\hat{\lambda} = \frac{N_{t+1}}{N_t} \quad (11.3)$$

We thus need to keep in mind the quantity being estimated. Using log-linear regression the logical estimate is r , while the ratio estimator gives λ directly. How important is the difference? If the rate of change is small, the two interpretations are nearly indistinguishable. But for larger rates of increase, the two interpretations are sufficiently different to make an appreciable difference in, say, projections of population size into the future. Fig. 11.2 exhibits the values of the two interpretations of λ .

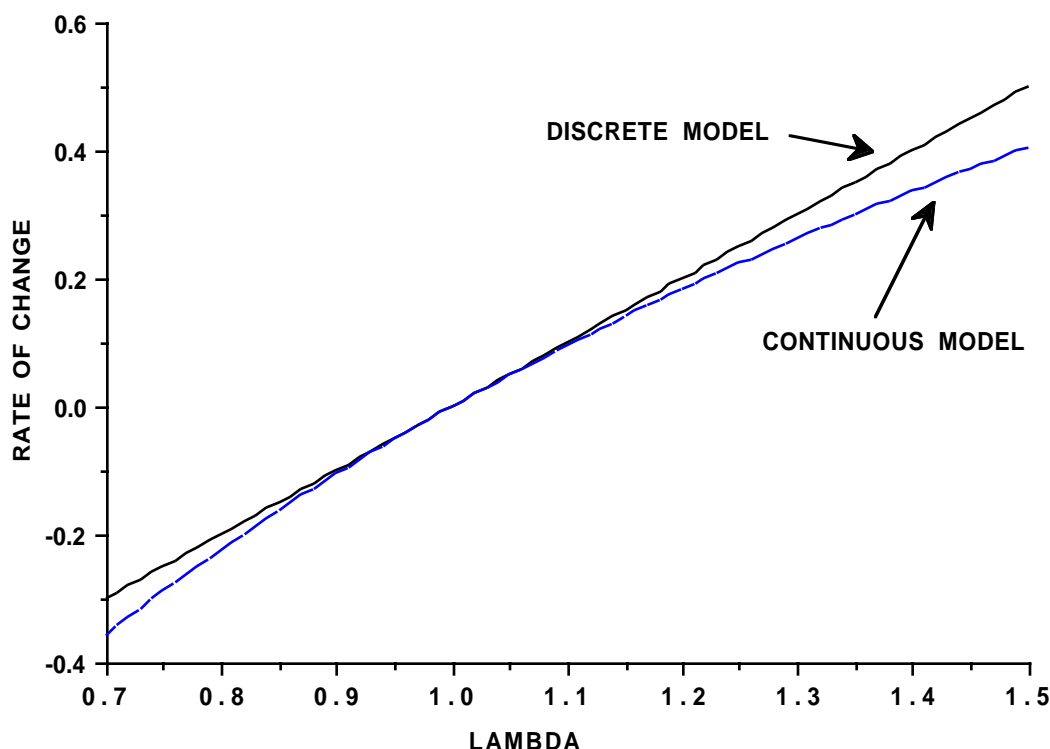


Fig. 11.2 values of r for the two interpretations of λ . The continuous model ($\lambda = e^r$) yields values appreciably lower than those for the discrete or geometric model ($\lambda = 1 + r$) when λ is significantly below or above 1.0.

Some discussions of the continuous model present the rate of increase as having two components, $r = b - d$, where b represents births and d , deaths. These are "instantaneous" rates, i.e., appropriate to indefinitely small increments of time. However, the model of Fig. 11.1 doesn't work that way. The model for the actual trend for one year could be written as:

$$N_{t+1} = N_t s^{52} R = N_t \lambda \quad (11.4)$$

where s is a weekly survival rate. In actuality, the model would be more complex, with s being a blend of rates over the year and R , the birth-pulse,

usually doesn't occur instantaneously. Nonetheless, eq. (11.4) describes the general pattern -- mortality occurs throughout the year, while reproduction occurs in a short annual period. The geometric approximation operates as a "step-function", assuming the population remains constant throughout the year, and then jumping to the new level at year-end.

One very important consequence of the birth-pulse model is that the basic unit of time is one year. This means that models for population growth need to be difference equation models, rather than the continuous models implied by the differential equations commonly presented in ecology textbooks. Differential equations are often derived as limiting expressions for difference equations. That is, a relationship is written as a difference equation with time unit Δt and then Δt is assumed to become very small, resulting in an "instantaneous" rate or differential equation. Thus, if the units of time become very small (days, perhaps, instead of years) the discrete model becomes nearly indistinguishable from the continuous model. This does not work with birth-pulse models, due to the fact that births occur only once a year. Consequently, the more realistic difference equation models are not necessarily suitably approximated by continuous models. However, it is often possible to obtain a perfectly reasonable fit of a continuous model to the data. Thus, in Fig. 11.1, if we observe population size annually just after births take place (or just before), the continuous exponential model (dotted line) fits the data very nicely. However, the rates of increase (r) implied by the two models may be quite different unless λ is in the neighborhood of unity (Fig. 11.2). In many situations, one can ignore these details by using eq. (11.1). Problems may come in at two points: (1) when estimating λ by eqs. (11.2) or (11.3), and when a more complex model for population growth is fitted.

11.3 Lotka's equation and the Leslie matrix model

The underlying model was derived by Lotka (1907) for continuously reproducing populations. Leslie (1945) derived his matrix formulation as an approximation to a continuously reproducing population, and the demographic textbook approaches (e.g., Keyfitz 1968) also focus on the continuous situation, since they are largely concerned with human populations, where reproduction occurs the year around. Keyfitz (1968:Ch.8) discussed convergence of the matrix equation to Lotka's integral equation. For practical purposes, it is useful to be able to inter-relate the discrete version of Lotka's equation (eq.(11.1)) with the Leslie matrix. This is readily done through the characteristic polynomial (characteristic equation) of the matrix, if the "maternity values" (F_x) of the Leslie matrix are expressed as $F_x = s_0 m_x$, where s_0 is survival from birth to age 1. This points up the main difference between the two formulations -- Lotka's equation pertains to the population just after reproduction occurs, while the Leslie matrix pertains to the population just before reproduction. That is, the first term of the stable age distribution (eq.(11.6)) is $c_0 = B$, the proportion of newborns in the population, while the first element in Leslie's population vector (n_1) represents the youngest age class, just before parturition takes place, and one year after births occur.

Cole (1954) showed that Lotka's integral equation can be replaced by a summation for populations in which births are concentrated in a relatively short period of the year. In practice, solutions of Lotka's equation have

necessarily been approximated by a summation, in any case. The basic equation is:

$$1 = \sum_{x=a}^w \lambda^{-x} l_x m_x \quad (11.5)$$

where l_x denotes survivorship from birth (or from recruitment to some older portion of the population) to age x , m_x represents age-specific reproductive rates, and the summation ranges from the age of first reproduction (a) to the maximum age (w) assumed represented in the population. Lotka's intrinsic rate of increase (r) is widely used, but is replaced here by using λ since a finite rate of increase is appropriate for the many species populations that reproduce in a short annual period ["birth pulse" populations in the useful terminology of Caughley (1977)]. One can thus interpret λ as e^r or $1+r$.

The results given here were derived for "birth-pulse" populations. Continuous breeding may take several forms. If the reproductive rate is constant throughout the year, then equation (11.5) can be used as an approximation, as was done by Birch (1948). If constant, continuous breeding occurs only over part of the year, with no reproduction at other times, then it may be necessary to resort to the approach of Leslie and Ranson (1940). In a third pattern, reproduction may take place at any time of the year, but there is a definite seasonal peak. Murray and Garding (1984) presented a general approach for populations with "discontinuous breeding seasons" that depends on an "average m_x " but this rate is defined only by the statement (Murray and Garding 1984:325) " m_x is the average fecundity of individuals in age class x , in the sense that the $C_x(t)$ individuals produce $C_x(t)m_x$ offspring between t and $t+1$ that are observed alive at $t+1$...", and no method for calculating this "average m_x " was given in the paper. Consult Caswell (1989, 2001) for more explicit approximations.

Lotka's model, in the form given by Cole (1954), represents the population just after births take place. If we consider the population structure just before the annual period of parturition, the characteristic polynomial of the Leslie (1945) matrix gives the same result. The Lotka equation (eq. (11.5)) is somewhat easier to write out and preserves the central (l_x) entry of the traditional life table. To construct a Leslie matrix, one only needs to note that Leslie's reproductive rates can be written as $F_x = s_0 m_x$, where s_0 = survival from birth to age 1 (Eberhardt 1985). Annual survival rates appear in the Leslie matrix as $s_x = l_{x+1}/l_x$ (hence $s_0 = l_1$). It is important to note that the calculations here assume first-year survival (s_0) to be independent of fate of the adult female. Caswell (1989, 2001) gave definitions of the F_i that permit structuring the Leslie matrix for censuses of "birth-pulse" populations taken at any time of the year, but this requires some approximations. He also considered birth-flow populations, and devoted most of the books to "stage-structured" models, which are applicable when ages cannot readily be assigned to individuals.

11.4 The stable age structure

The stable age distribution is calculated as:

$$c_x = B \lambda^{-x} l_x \quad (11.6)$$

because c_x represents proportions summing to unity, we have

$$B = \frac{1}{\sum_{x=0}^w \lambda^{-x} l_x}$$

1.5 Augmented life tables

An "augmented" life table is simply a convenient way to present the data for Lotka-Leslie calculations in table form. Basic data for an augmented life table are a column of ages, and the l_x , m_x , and c_x columns. Iterative solutions of eq.(11.5) are needed to determine the rate of increase (λ or r) and to calculate c_x . Such solutions are readily obtained with a simple computer program (or on a programmable calculator). A convenient alternative is to incorporate the data in a spreadsheet program that includes a column of values of $\lambda^{-x} l_x m_x$. Trial and error calculations can then be used to satisfy eq.(11.5). However, many of the currently available spreadsheet programs include iterative procedures, so the table can be set up to provide a direct solution of eq.(11.5). This can readily be done with the "SOLVER" routine in EXCEL (found in the TOOLS menu). The column of $\lambda^{-x} l_x m_x$ values should nonetheless be maintained, since it is both a convenient way to examine approximations and provides useful information, described below. One of the convenient features of the spreadsheet approach is that the data can often be transferred directly into graphics and word processing programs. At least one of the commercially available spreadsheet programs (EXCEL) also incorporates routines for using matrix equations, so that various further operations on the Leslie matrix are feasible directly from an augmented life table, if desired. For most practical purposes, the Leslie matrix is not needed. The term, "augmented", is likely superfluous, as most contemporary writers now simply use "life table" to include reproduction, although the original meaning concerned only survivorship.

11.6 An augmented life table

The example used here (Table 11.1) is based on data on elk (*Cervus elaphus*) reported by Houston (1982). The survivorship data given by Houston (1982:Table 5.8) were fitted to an equation given by Eberhardt (1985:eq.(6)) by nonlinear least-squares on logarithms of the survival data (Fig. 11.3). The equation used is:

$$l_x = \exp[-a_1 - a_2 x - a_3 (\exp(b_3 - 1))] \quad (11.7)$$

Reproductive data (Fig. 11.2) from Houston (1982: Tables 5.1 and 5.2) were used with eq (11.8), developed by Eberhardt (1985):

$$m_x = a[1 - \exp(b(x - c))]\exp[-a_3 \exp(b_3 x - 1)] \quad (11.8)$$

Pregnancy rates for older animals were obtained as a weighted average of the 1962-1967 data given by Houston (1982: Tables 5.1 and 5.2). Data for the older elk were reported as an average for all animals 16 years of age and older, and are arbitrarily plotted here at age 18.

There is now a considerable degree of confusion in the literature about parameter definitions, which is too extensive and too pervasive to discuss in detail here. Jenkins (1988) provided a good review of the confusion in textbooks. David (1995) more recently reviewed different formulations of eq. (11.5). Much of the difficulty stems from the fact that both the Lotka and the Leslie approaches actually refer to continuously-breeding populations, but are computed with discrete approximations. Definitions of continuously breeding populations thus involve averaging over some time period, usually one year in length. The present approach depends on Cole's (1954) development of the "Lotka" equation as a discrete model where reproduction is assumed, in effect, to occur instantaneously at the same time every year.

Applications of the augmented life table to actual field data must, in nearly all cases, use that data which can be obtained on a particular population. "Birth rates" are then often actually observed as pregnancy rates. Much of the confusion as to definitions (e.g., "natality", "fecundity") and differences between the Lotka and Leslie models can be avoided in practice simply by computing both approaches. This is readily accomplished by spreadsheet methods.

All that is needed is to multiply the c_x column (stable age distribution) of Table 11.1 by an initial population size (N_0). These values can then be projected forwards one year by multiplying by entries in the s_x column to create a column (N_1) of projected numbers in age classes 1,2,3,... . The first entry in N_1 (age class zero) is obtained as the sum of products of the m_x entries (Table 11.1) with those in column N_1 (in most spreadsheets it is convenient to enter the individual products in an intermediate (B_1) column). The same procedure may be used to project N_1 to N_2 , N_2 to N_3 , and so on. The overall procedure is essentially that of the Leslie projection matrix, yielding the corresponding series of population vectors (N_1, N_2, N_3, \dots). The only difference, apart from a lack of matrix notation, is that newly-born individuals are represented by an entry, whereas they do not appear in the age vectors of a Leslie matrix projection.

The projection calculations should carry forward fractional "animals". If this is done, then the ratio of successive sums will yield the same value of λ as obtained by solution of eq (11.5). It is instructive to round the projection vector (N_i) entries (readily done by a standard spreadsheet command) and calculate a series of λ_i . For small and moderate population sizes such a calculation gives a worthwhile illustration of the desirability of including no more than 2 decimal places in reporting estimated values of λ . For example, the data of Table 11.1 were used to project an initial elk population of 1,000 individuals. With fractional entries, the successive ratios of column sums are all 1.20133, but if rounding to the nearest "individual" in each age-class is used, successive values are 1.2010, 1.1998, 1.1964, 1.1972, 1.2010, 1.2000, 1.2013, 1.2012, 1.1989, and 1.2005. Note that, in calculating λ by eq.(11.5), one will

usually carry more than 2 decimal places in order to be sure that eq.(11.5) "balances".

Table 11.1 Augmented life table for elk data from Houston (1982)

Age	Reproductive rate $m(x)$	Survivorship $l(x)$	Adjusted net maternity rate	Stable age distribution $c(x)$	Survival rate $s(x)$
0	0	1	0	0.2426	0.6745
1	0	0.6745	0	0.1362	0.995
2	0.0749	0.6711	0.0348	0.1128	0.995
3	0.4682	0.6677	0.18031	0.0934	0.9934
4	0.4732	0.6634	0.1507	0.0773	0.994
5	0.4728	0.6594	0.1246	0.0639	0.9936
6	0.4721	0.6552	0.1029	0.0529	0.9929
7	0.4711	0.6505	0.0849	0.0437	0.9918
8	0.4696	0.6452	0.0698	0.0361	0.9903
9	0.4674	0.6389	0.0573	0.0297	0.988
10	0.4641	0.6312	0.0468	0.0245	0.9845
11	0.4592	0.6215	0.0379	0.02	0.9795
12	0.452	0.6087	0.0305	0.0163	0.9719
13	0.4416	0.5916	0.0241	0.0132	0.9608
14	0.4264	0.5685	0.0186	0.0106	0.9445
15	0.4048	0.5369	0.0139	0.0083	0.9208
16	0.3746	0.4944	0.00983	0.0064	0.8865
17	0.3337	0.4383	0.0065	0.0047	0.8377
18	0.281	0.3671	0.0038	0.0033	0.77
19	0.2174	0.2827	0.0019	0.0021	0.6791
20	0.1484	0.192	0.0007	0.0012	0.5632
21	0.084	0.1081	0.0002	0.0006	0.4261
22	0.036	0.0461	0	0.0002	0.2813

The "adjusted net maternity rate" is:

$$\lambda^{-x} l_x m_x$$

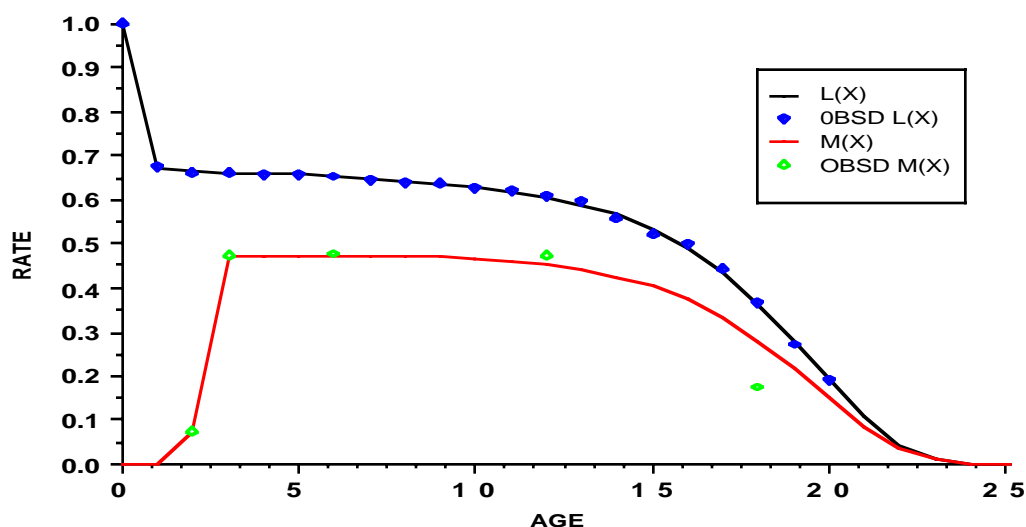


Fig. 11.3. Survivorship (upper curve) and reproductive data for elk from Houston (1982). Fitted curves (eqs. (11.7) and (11.8)) are shown, along with estimated age-specific rates (m_x rates were averaged for some age groups).

11.7 Reproductive and survival curves

The Lotka-Leslie model depends on age-specific rates. Ideally, λ would be calculated from eq. (11.5) using estimates of reproductive (m_x) and survivorship (l_x) rates for each age class, and the models are often presented as if such individual age-class values were available. In practice, however, we seldom have the large volume of data necessary to estimate rates for each age-class, and some kind of averaging has to be employed. Because the l_x values are calculated as the product of individual survival rates such curves always appear smooth, even though the actual survival estimates may be very erratic. It is thus desirable to also plot individual survival rates.

In practice, fitting curves like those of eqs. (11.7) and (11.8) may not be particularly useful or desirable. Very likely their main utility lies in comparing different data sets and in dealing with the issue of senescence. Because sample sizes are usually small, very few older individuals will be observed so that little will be known about senescence in a given species. In many studies, the possibility of lower reproductive and survival rates in the older age classes has simply been ignored. For large vertebrates with relatively high adult survival rates this practice can introduce a significant bias.

The practical way to limit such a bias is simply to truncate the age distribution, i.e., to choose a value of the maximum age (w) used in eq. (11.5) below the maximum age actually observed for a given species. Very likely the main value of fitting curves to reproductive and survivorship data is just to demonstrate the impact of various choices of w on the resulting estimate of λ . In many cases there may not be enough data to make a guess at w , so that it may be helpful to review data on other species, as shown in Fig. 11.4 below.

11.8 Some useful approximations

The approximation used here serves when individual age-specific rates cannot be obtained for all age-classes, as usually is the case in practice. It represents survivorship by $l_x = l_a s^{(x-a)}$ (when $x \geq a$) and reproductive rate by $m_x = m$, so that the net maternity curve is $l_x m_x = m l_a s^x$, where l_a denotes survival to the age of first parturition, and s denotes adult survival rate. Senescence is approximated by truncating the net maternity curve, i.e., w in eq.(11.5) is reduced to compensate for dropping the senescence terms of eqs. (11.7) and (11.8). Lotka's equation (eq.(11.5)) then has the solution used by Eberhardt (1985:eq.(9)), expressed here as a polynomial in λ :

$$\lambda^a - s\lambda^{a-1} - l_a m \left[1 - \left(\frac{s}{\lambda}\right)^{w-a+1}\right] = 0 \quad (11.9)$$

when w becomes very large we have:

$$\lambda^a - s\lambda^{a-1} - l_a m = 0 \quad (11.10)$$

If $\lambda = 1$, then $l_a m = 1 - s$, so that recruitment to reproductive age just balances annual mortality $(1-s)$, as required for stationarity. Because 1 or 2 of the younger age classes often show sharply lower reproductive rates than older animals, one may need to use 2 or 3 values of m , rather than the single value of eq.(11.9) for accuracy in the approximation. The polynomial of eq.(11.9) then becomes somewhat more complicated, but is not needed in practice, as the relevant entries can simply be introduced in a spreadsheet table like Table 11.1 for a solution.

When some of the subadult age classes can be assumed to have the same survival rate (s) as adults, eq. (11.9) can be written in terms of survival to age k (as l_k) after which survival is at the adult rate, so that $l_a = l_k s^{a-k}$, giving:

$$\lambda^a - s\lambda^{a-1} - l_k s^{a-k} m \left[1 - \left(\frac{s}{\lambda}\right)^{w-a+1}\right] = 0 \quad (11.11)$$

Utility of the approximations can be assessed by comparing the adjusted net maternity curve for the approximate values with values for the fitted equations (eqs.(11.7) and (11.8)). For the elk data discussed above, the approximation is very good (Fig. 11.4). Using the data on fur seals (*Callorhinus ursinus*) of Eberhardt (1985) gives a little poorer fit (Fig. 11.5), but nonetheless a good approximation.

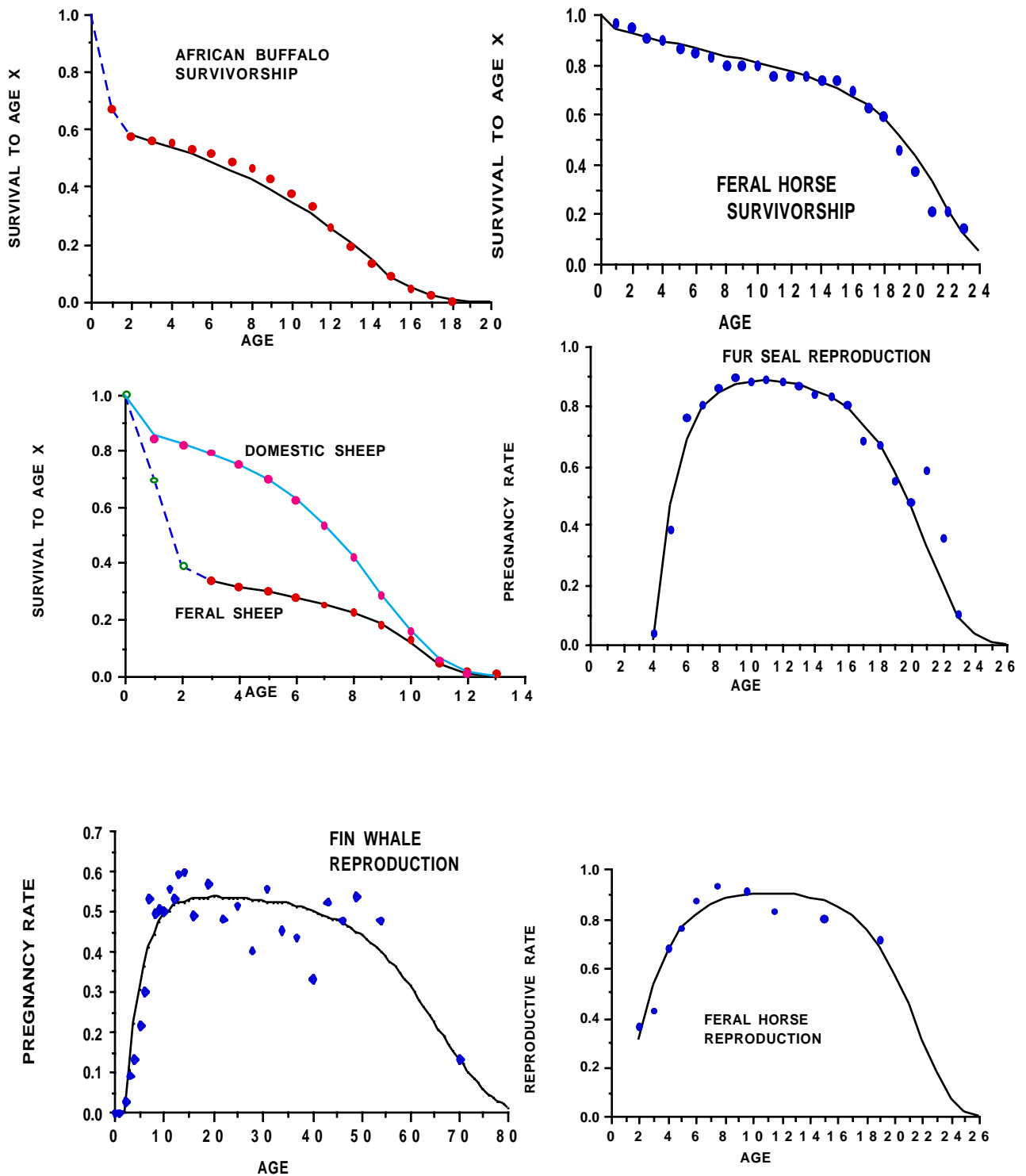


Fig. 11.4. Examples of survivorship and reproductive data. The domestic sheep data are from Hickey (1960), while the feral sheep data are from Grubb (1974). These curves show the impact of mortality early in life on a wild population

very nicely. The feral horse survivorship data are from Garrott and Taylor (1990), while the horse reproductive data are from Berger (1986). The African buffalo survivorship data are from Sinclair (1977), the fur seal data from Eberhardt (1981), and the fin whale data from Mizroch 1981.

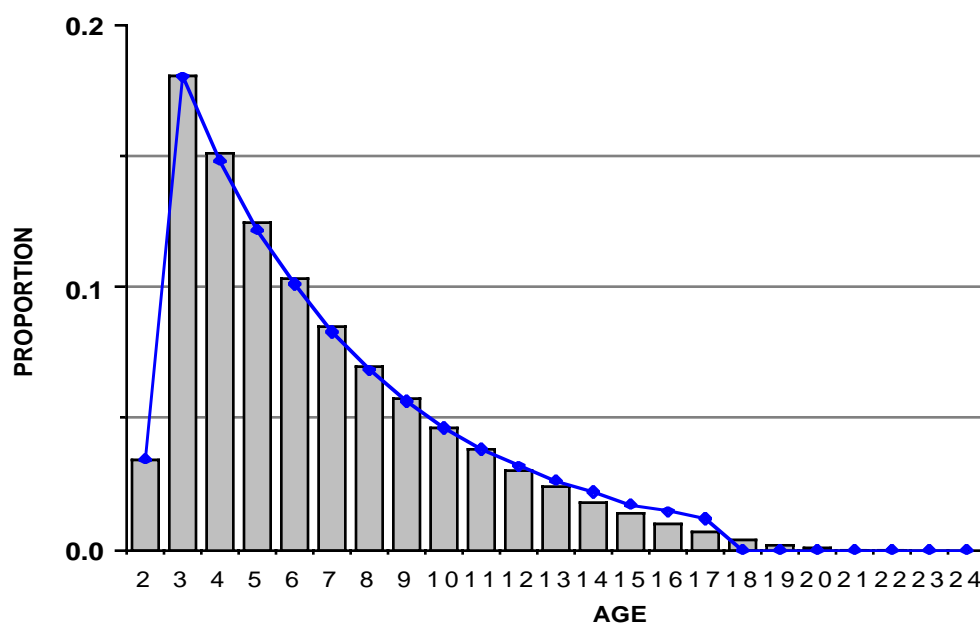


Fig. 11.5 Approximation (solid points) compared to values (bars) from fitted curves (eqs.(11.7) and (11.8)) for elk data from Houston (1982).

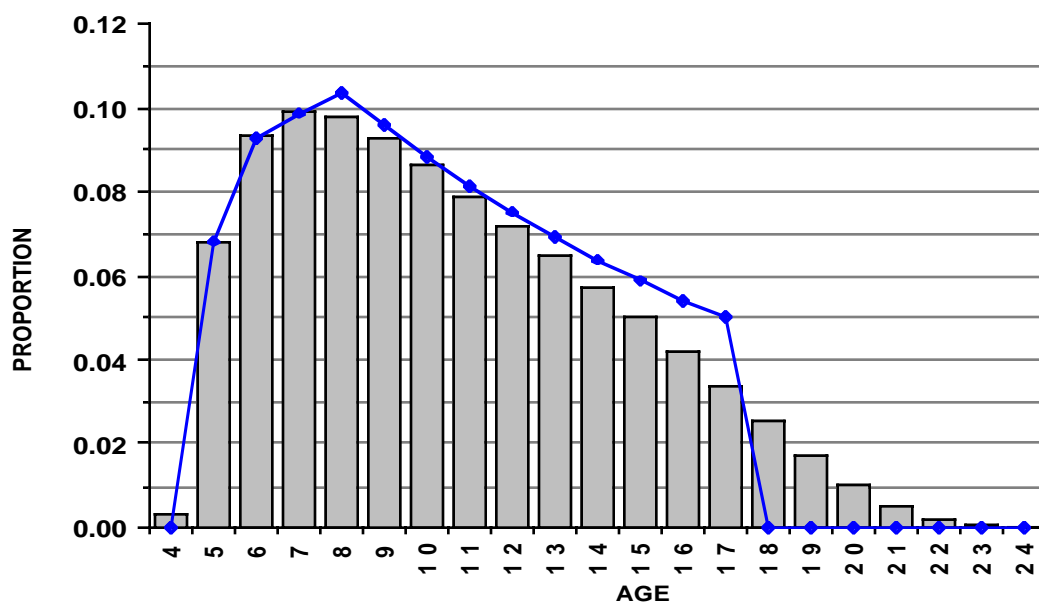


Fig. 11.6. Approximation (solid points) compared to data from fitted curves obtained by Eberhardt (1985) for data on northern fur seals.

11.9 Approximate variance of λ

Setting confidence limits on λ is likely best done by the statistical technique of bootstrapping. However, bootstrapping does not supply estimates

of the relative magnitude of the several components contributing to the overall variance. Such estimates are essential in planning studies, i. e., how much effort should be devoted to estimating each component, and what total effort is required to produce a given width to the confidence interval? Questions of this kind can be approached by approximating the variance of λ by the "delta method".

A general expression for obtaining a variance by the delta method is (Seber 1982):

$$V[g(x)] \approx \sum_{i=1}^n V(x_i) \left(\frac{\partial g}{\partial x_i} \right)^2 + 2 \sum_{i < j} \text{cov}(x_i, x_j) \left(\frac{\partial g}{\partial x_i} \right) \left(\frac{\partial g}{\partial x_j} \right) \quad (11.12)$$

where $g(\mathbf{x})$ is some function of several variables, x_i , $v(x_i)$ is the variance of a given x_i , $\frac{\partial g}{\partial x_j}$ represents the partial differential of $g(\mathbf{x})$ with respect to x_j , and $\text{cov}(x_i, x_j)$ denotes the covariance of two variables x_i and x_j . In the cases considered here, it is assumed that these covariances are zero or negligible.

The partial derivatives provide a useful byproduct, in that their numerical values give an indication of the relative importance of each component variable in determining λ . The partial derivatives have to be obtained by implicit differentiation, due to the fact that there is no "closed form" expression for λ , i. e., $\lambda = g(\mathbf{x})$ cannot be written as a simple mathematical expression (λ is estimated by iterative methods from eq.(11.5), (11.9), (11.10), or (11.11)). Inasmuch as the partial derivatives are complicated, they are most conveniently obtained by one of the computerized routines now available for equation solving. Results for eq (11.9) are:

$$\frac{\partial \lambda}{\partial s} = \lambda[(w-a+1)l_a m \lambda \left(\frac{s}{\lambda}\right)^{w-a+1} - s \lambda^a] / sA \quad (11.13)$$

$$\frac{\partial \lambda}{\partial l_a} = m \lambda^2 \left[\left(\frac{s}{\lambda}\right)^{w-a+1} - 1 \right] / A$$

$$\frac{\partial \lambda}{\partial m} = l_a \lambda^2 \left[\left(\frac{s}{\lambda}\right)^{w-a+1} - 1 \right] / A$$

where $A = (w-a+1)l_a m \lambda \left(\frac{s}{\lambda}\right)^{w-a+1} + \lambda^a (as - s - a\lambda)$.

Recently there has been a considerable amount of interest in "sensitivity" and "elasticity". Sensitivity has been defined as the partial derivative of λ with respect to a_{ij} and elasticity as:

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

These definitions refer to the individual elements, a_{ij} , of a Leslie matrix, whereas equations (11.13) are based on implicit differentiation of eq. (11.9). Nine papers in a Special Feature in vol. 18(3) of the journal, Ecology, describe

recent developments. These papers nearly all require matrix algebra and use "stage-structured" models extensively.

Using the delta method requires variance estimates for each component of the equation used. The main use at present appears likely to be in planning a study, or in deciding how to improve a given data set by collecting more observations. One then might assume a binomial distribution for the survival rates for planning purposes. Obtaining a simple variance formula (like the binomial) for reproductive rates is a subject that needs further investigation. More research is also needed to evaluate the accuracy of both the delta method and bootstrapping when used with the Lotka-Leslie model. Two approaches are used here. One is to compare the two methods on actual data sets for several species, and the second is to test the methods by monte carlo simulations.

Bootstrapping is a relatively new statistical technique that takes advantage of the "number-crunching" ability of modern computers. The ability to do many thousands of computations very quickly makes it feasible to "resample" a data set and extract variance estimates. The surprising feature of bootstrapping is that useful results appear to be available for quite small samples.

The approach used here to set confidence limits on λ is reasonably simple, and can be illustrated with reference to eq. (11.9). For simplicity, suppose n_1 observations are available for estimating s , n_2 for l_a , and n_3 for m , and stored in computer files. Exactly n_1 random draws with replacement are made from the file of data for s ("with replacement" means that the same data point can be drawn more than once). An estimate of s is then made from this sample by whatever technique was used for the original estimate. The same process is carried out for l_a and m , using n_2 and n_3 samples drawn with replacement, and an estimate of λ formed from the resulting data.

The technique for forming confidence intervals used here consists in repeating the above scheme a large number of times, say 1,000. The resulting 1,000 estimates are arranged in a frequency distribution, and confidence limits are determined as the points on the frequency distribution that cut off approximately $\alpha/2$ of the observations in each "tail" of the distribution, with α usually set at 0.05. Thus for 1,000 bootstraps, the confidence limits are the points cutting off the smallest 25 observations (lower confidence limit) and the largest 25 observations (upper confidence limit). This is the "percentile" method (Efron and Tibishirani 1993: Ch. 13).

An alternative approach is to use the set of bootstrap estimates to calculate a standard deviation (s), and set approximate 95% confidence limits as the original estimate of $l \pm 1.96 s$. This technique has also been applied to the examples described below, and in the monte carlo simulations, and gave results very close to the percentile method.

Most of the applications described below have been based on eqs. (11.9) through (11.11), and values of a and w were assumed known. Given enough appropriately collected data, one can bootstrap eq. (11.5) directly. Results for one example appear below, along with examples depending on the approximations given above.

11.10 Examples of bootstrapping

The following figures show examples of bootstrapping for a number of species.

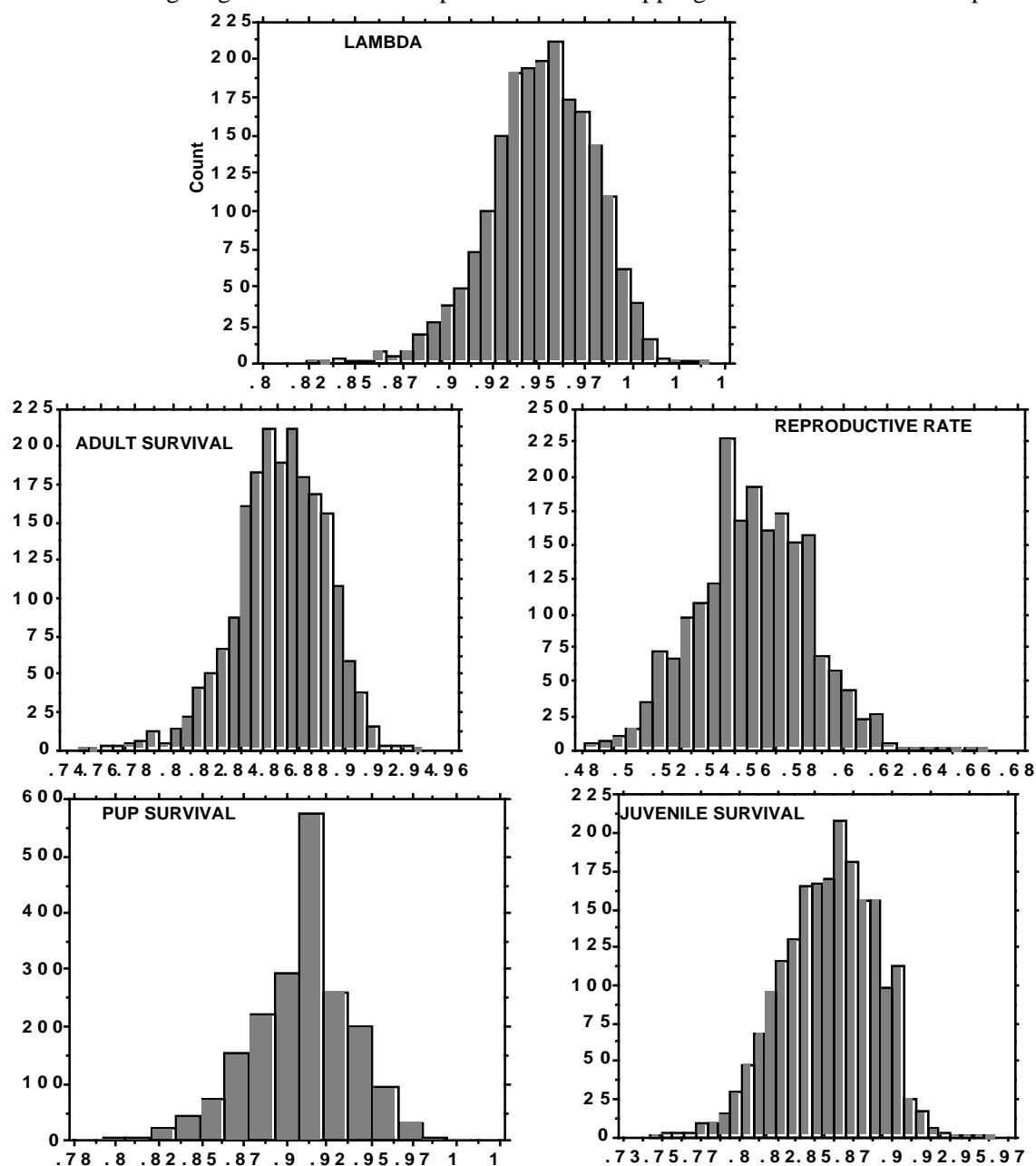


Fig. 11.7. Outcome of bootstrapping survival and reproductive data for the Hawaiian monk seal on Laysan Island. The reproductive and survival data were described by Johanos et al (1994) and Gilmartin et al. (1994). Frequency distributions for the components of eq. (11.5) are shown here. In this instance, the adult survival rate was assumed to apply from age 1 onwards, so that $k = 1$. Early survival has 2 components, survival from birth to weaning, and from weaning to age 1. The estimated value of λ was 0.97, with 95% confidence limits of 0.91 to 1.01. The indicated rate of decline in the population was supported by a log-linear regression on trend data, which gave essentially the same value of λ .

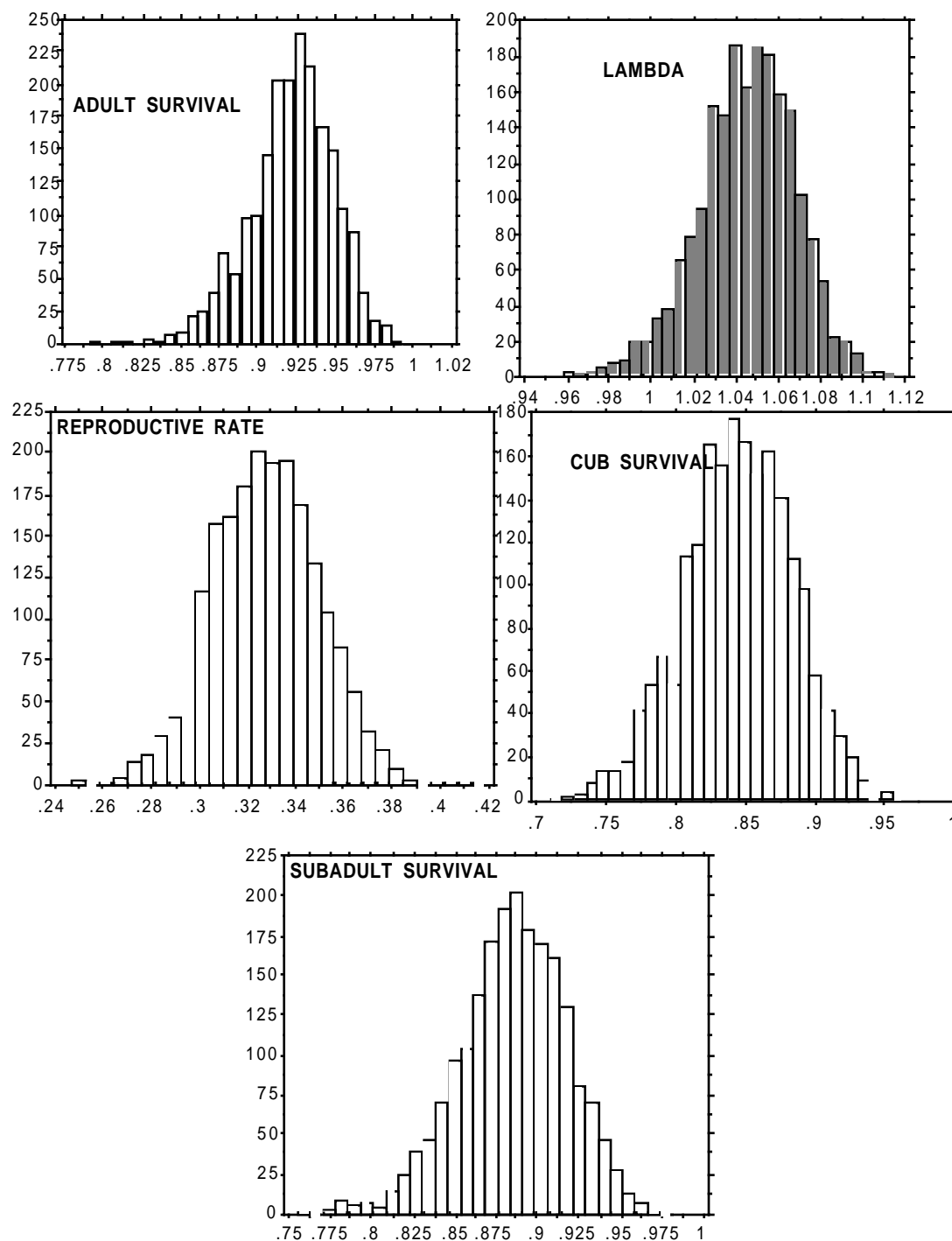


Fig. 11.8. Bootstrapping data from grizzly bears in the greater Yellowstone area. Details of the study were reported by Eberhardt et al. (1994). In this example, two subadult rates were used, so that $l_a = s_0 s_1^4$, where s_0 = cub survival, and s_1 = annual subadult survival rate. Cub survival is appreciably less than subadult survival, which in turn is less than adult survival.

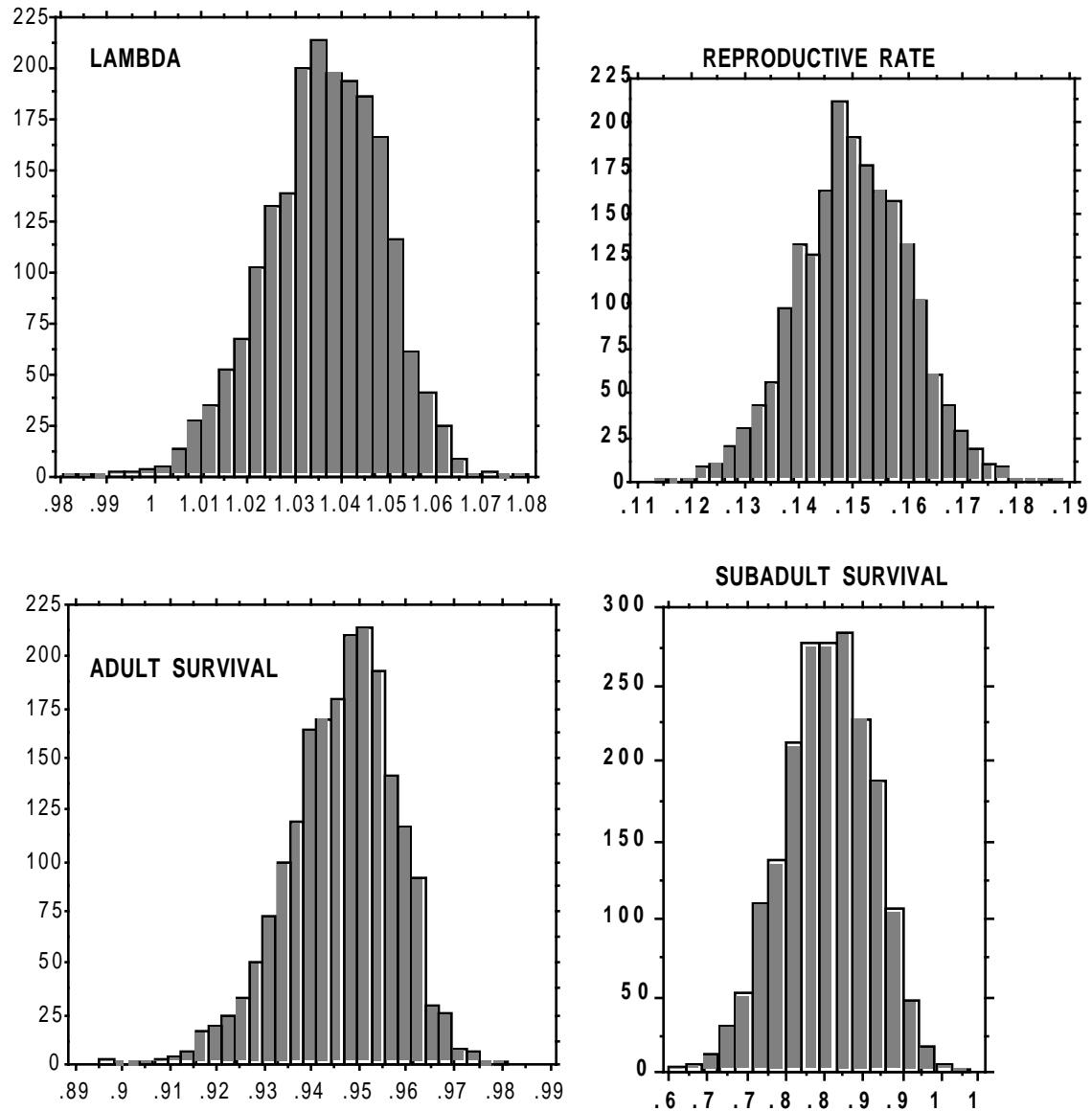


Fig. 11.9. Bootstrapping data for Florida manatees. Manatees reproduce at about 3 year intervals, and thus high adult survival is essential for population growth.

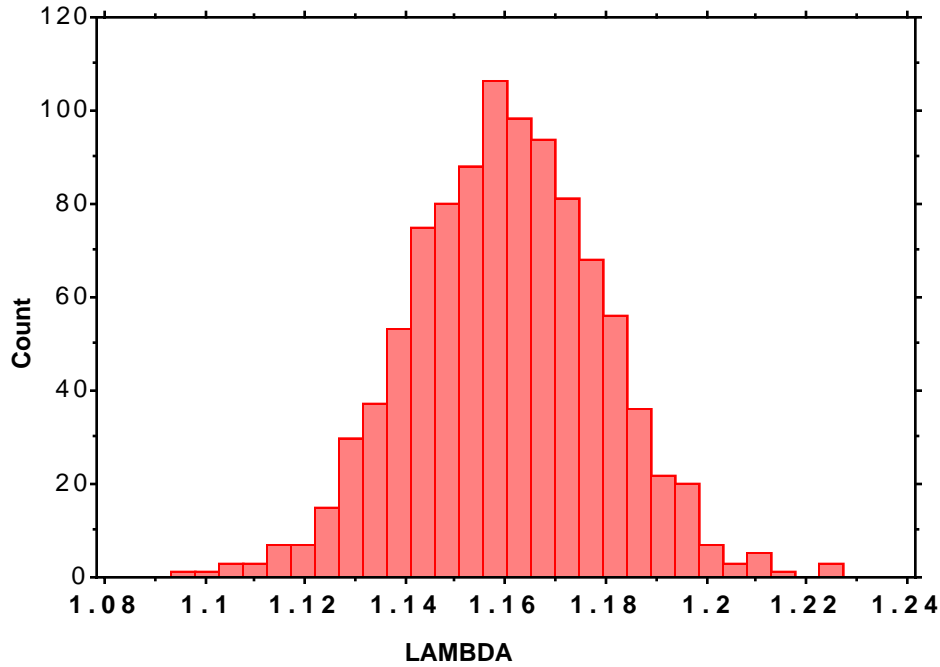


Fig. 11.10. A study of feral horses by Garrott and Taylor (1990) provides sufficiently extensive data for bootstrapping eq. (1) directly. The frequency distribution of λ above is from 1,000 bootstraps of Pryor Mountain horse data. The 95% confidence limits were 1.122 to 1.196.

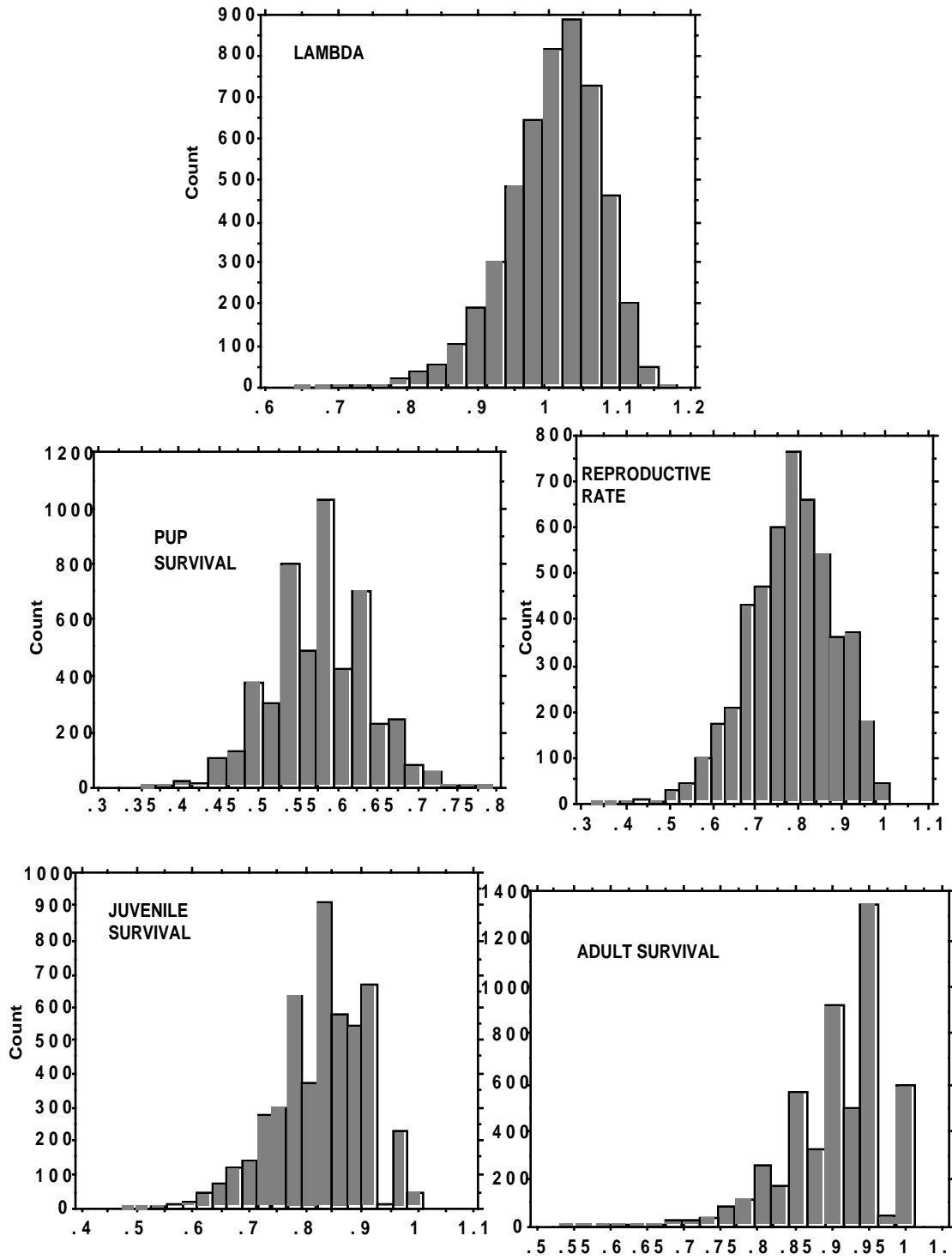


Fig. 11.11. Bootstrapping data from a study of California sea otters. Data largely from Siniff and Ralls (1991).

11.11 Delta method examples

Applying the delta method of eq.(11.12) to data on actual populations gives the results shown in Table 11.2.

Table 11.2 Data from the delta method for actual populations.

		Monk seals	Grizzly bears	Manatees	Feral horses	Sea otters
Survival to age k	l k	0.38	0.52	0.68	0.968	0.63
Reproductive rate	m	0.28	0.33	0.15	0.282	0.23
Adult survival	s	0.87	0.92	0.95	0.974	0.91
Age first reproduction	a	6	5	4	3	3.5
Maximum age	w	20	20	50	20	15
Lambda						
Bootstrapping		0.97	1.046		1.161	1.013
Delta method		0.97	1.046		1.158	1.006
Coefficients of variation						
Delta method		0.03	0.02	0.01	0.009	0.07
Bootstrapping		0.03	0.02	0.01	0.017	0.07
Components of variance						
Survival		0.96	0.44	0.58	0.21	0.81
Early survival		0.02	0.46	0.18	0.03	0.1
Reproduction		0.02	0.1	0.24	0.76	0.09
Total		1	1	1	1	1
Partial derivatives						
Survival		1.1	0.57	1.02	1.03	0.9
Early survival		0.11	0.2	0.09	0.16	0.17
Reproduction		0.3	0.32	0.5	0.55	0.56

11.12 Comparisons with direct estimates of λ

From Table 11.2 it appears that the delta method and bootstrapping yield much the same estimates of λ and variability. One might thus use bootstrapping to obtain confidence limits and utilize the delta method to examine components of variance as a guide to improving estimates of λ by obtaining larger samples of data on the parameters that contribute most to overall variability. Thus in Table 11.2 the main improvement for monk seals will come from obtaining more information on adult survival, which seems often to be the case. However, the grizzly bear data suggest improvements might be equally important for both early and adult survival. For the particular feral horse herd used in the example, it appears that more data on reproduction should be obtained, but this likely is an exception to the general rule due to circumstances.

An important further check on the estimates of λ obtained from the approximations obtained above is to compare estimates of λ from reproductive and survival data with those obtained from direct measures of population size, usually by log-linear regression following the examples of Chapter 9. Fig. 11.12 shows results of such a comparison. The line shown in Fig. 11.2 is a 1:1 line, i.e., shows exact agreement of the 2 estimates. The major discrepancy appears to be the data for caribou, and it seems likely that it is due to underestimation of adult female survival rates, inasmuch as they were reported to be significantly lower than those for subadults.

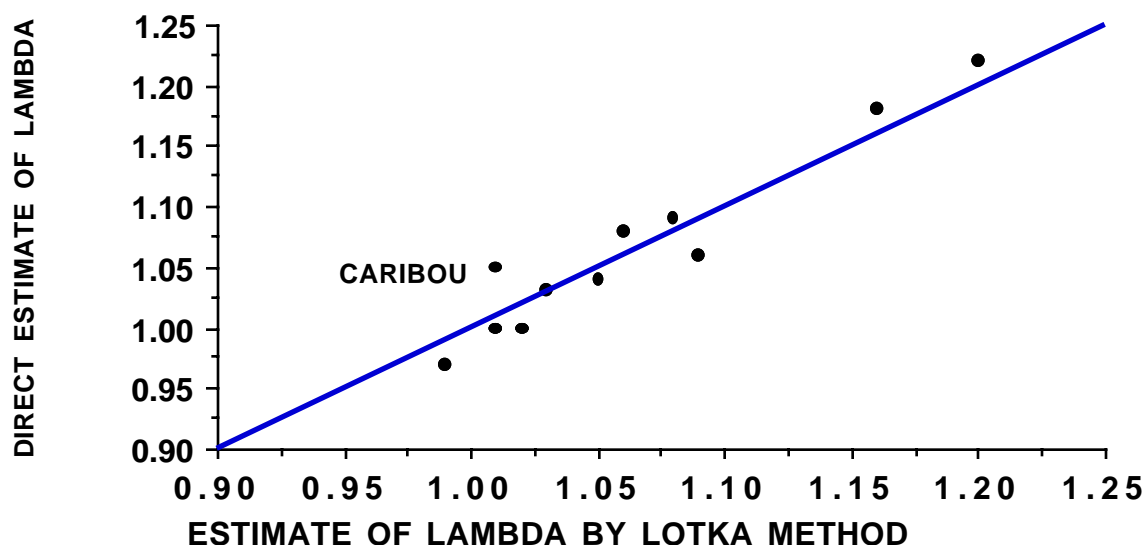


Fig. 11.12. Comparison of direct estimates of lambda with those obtained from reproductive and survival data by the Lotka method. Thirteen examples are plotted of which 2 coincide with other points.

11.13 Development of stable age-structure

The following material gives a simple approach to development of the Lotka equations. A formal proof requires methods of the calculus on a Complex domain. The derivation used here assumes the end result, so does not consist of a "proof" but is rather a simple demonstration of the mechanics of the process. A further simplification is to assume time units of one year and to regard reproduction as occurring instantaneously at the beginning of each year. We also assume that the population is growing geometrically at a rate, r . Thus we have:

N_0 = initial population

rN_0 = number added in first year

$N_1 = N_0 + rN_0 = N_0(1 + r)$ = population at end of first year

$N_2 = N_1 + rN_1 = N_0(1 + r)^2$ = population at end of second year

and, generally:

$$N_t = N_0(1 + r)^t = \text{population at end of } t^{\text{th}} \text{ year} \quad (11.14)$$

The above equation admits the possibility of fractional animals, which is not a matter of great concern if the population size (N_i) is large enough to

avoid the influence of chance fluctuations. There are advantages in keeping fractional animals and thus regarding the values calculated as expectations.

A convenient tabulation of the process has time (in years) along the left margin and the series of year-classes along the top. A further simplification is achieved by supposing that a constant fraction (q) of the animals are lost each year so that $1-q = p$ survive to the next year. It should be noted that this is not a necessary assumption, but is used here to avoid complications. The first two years are shown as:

	Year-class				Total
<u>Time</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>population</u>
0	1				1
1	p	q+r			1+r

Thus the first age-class, at time zero, might be regarded as a "pioneer" generation in a new habitat -- or, equivalently, as some particular segment of a larger population. A fraction, p , of this initial group survives to year 1, as shown at time 1, under year-class 1. Since it is postulated that the population increases to $1+r$ at the end of the first year, it is necessary to add $q+r$ new recruits -- q to replace mortality in the "pioneer" group, and r to achieve the requisite increase. Going into the second year, the table is:

	Year-class				Total
<u>Time</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>population</u>
0	1				1
1	p	q+r			1+r
2	p^2	$p(q+r)$	$(q+r)(1+r)$		$(1+r)^2$

Fate of the pioneers is simply that another fraction (p) survives to year 2, as happens to year class 2. The entry in column 3 contains items to replace the losses, that is $p-p^2$ and $q+r - p(q+r)$. Since $q + p = 1$, this reduces to

$$p-p^2 + q+r - p(q+r) = q(1+r)$$

and we require that the previous year's total $(1+r)$ be increased by a fraction r to sustain the geometric rate of increase. Hence year-class 3, which contains all of that year's recruits, has to be:

$$q(1+r) + r(1+r) = (q+r)(1+r)$$

which gives the second year total (adding along the second row) as $(1+r)^2$.

The third year population is constructed in the same way, giving:

	Year-class				Total
<u>Time</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>population</u>
0	1				1
1	p	q+r			1+r
2	p^2	$p(q+r)$	$(q+r)(1+r)$		$(1+r)^2$
3	p^3	$p^2(q+r)$	$p(q+r)(1+r)$	$(q+r)(1+r)^2$	$(1+r)^3$

and a general formula for the i th year can be written down as:

$$\text{Total population} = p^i + p^{i-1}(q+r) + p^{i-2}(q+r)(1+r) + p^{i-3}(q+r)(1+r)^2 + \dots + p^{i-k}(q+r)(1+r)^{k-1} + \dots + p(q+r)(1+r)^{i-2} + (q+r)(1+r)^{i-1} = (1+r)^i$$

where i is the last year considered and k denotes a general term for some intermediate year class. Dividing through by the total population, $(1+r)^i$, gives the proportion in each year-class in year i :

$$\left[\left(\frac{p}{1+r}\right)^i + \frac{q+r}{1+r} \left\{ \left(\frac{p}{1+r}\right)^{i-1} + \left(\frac{p}{1+r}\right)^{i-2} + \dots + \left(\frac{p}{1+r}\right)^{i-k} + \dots + \left(\frac{p}{1+r}\right) + 1 \right\} \right] = 1 \quad (11.15)$$

Note that p is less than unity, so $p/1+r$ is also a fraction, hence large powers of this quantity tend to become vanishingly small. Hence, once i becomes large, the "pioneer generation" virtually vanishes, as do the other early year-classes, and the quantity in brackets approaches an infinite geometric series (but written backwards). Using the equation for the sum of a geometric series:

$$1 + x + x^2 + x^3 + \dots = (1-x)^{-1} \quad (x < 1)$$

we thus can write equation (11.15) as approximately:

$$\frac{q+r}{1+r} \left[1 - \frac{p}{1+r} \right]^{-1} = \frac{q+r}{1+r} \frac{1+r}{q+r} = 1$$

and the proportion corresponding to the x^{th} year class is:

$$c_x = \frac{q+r}{1+r} \left[\frac{p}{1+r} \right]^x \quad (11.16)$$

The quantity $\frac{q+r}{1+r}$ in equation (11.16) is also the ratio of any year's recruits to that year's population total (consider the last year-class entry in any row of the tables above), hence we denote it as

$$b = \frac{q+r}{1+r} \quad (11.17)$$

and regard this as the "birth-rate" per head (really a recruitment-rate).

Since survival from year-to-year is constant, the survival for x years is p^x , and equation (11.16) can be rearranged to

$$c_x = b(1+r)^{-x} p^x \quad (\Sigma c_x = 1) \quad (11.18)$$

11.14 Lotka's equations

In the development thus far, we have each year arbitrarily introduced the number of recruits required to sustain a population increasing geometrically, and this turned out to be a constant fraction (b) of the

population total. If we now assign age-specific reproductive rates, m_x , to each age-class ("year-class" above), an equation for b is:

$$\text{reproductive rate} = b = \sum_{x=0}^{\infty} c_x m_x \quad (11.19)$$

That is, b is the recruitment-rate per head and it is contributed to at a rate m_x , by each proportion of the population, c_x . Of course m_x may be zero, since the early and late age-classes may not reproduce. However, whether or not reproduction occurs in the first age-class depends on the species and the definition of time of recruitment, which might conceivably be set at sexual maturity. Using infinity for the upper limit of summation in equation (11.6) is a convenient convention and avoids the necessity for defining an upper limit to survival. When actual examples are considered, we replace it with w , the maximum age considered in an analysis.

If the definition of c_x given by equation (11.14) is inserted in equation (11.15) we have:

$$b = \sum_{x=0}^{\infty} b(1+r)^{-x} p^x m_x$$

or:

$$1 = \sum_{x=0}^{\infty} (1+r)^{-x} p^x m_x \quad (11.20)$$

and this now gives a general equation containing the several quantities involved in population analysis -- survival, reproduction, and rate of increase.

Recalling that the c_x are proportions summing to unity permits a useful rearrangement of equation (11.18), namely:

$$\frac{1}{b} = \sum_{x=0}^{\infty} (1+r)^{-x} p^x \quad (11.21)$$

Equations (11.18), (11.20) and (11.21) then provide tools for calculating the essential features of population structure. If reproductive and survival rates are known, a trial and error (iterative) solution of equation (11.20) gives the rate of population growth (r) to be expected when the population has reached the stable age-structure given by equation (11.18). Equation (11.21) provides a means for calculating b after equation (11.20) is solved.

The above equations suffer one obvious fault in that a constant rate of survival (p) has been assumed. However, the previously mentioned results of Lotka (1939) and Leslie (1945, 1948) permit replacement of the term p^x above by one that denotes an age-specific survival rate from recruitment to age x

(dated from the time of recruitment). Hence equations (11.18), (11.20) and (11.21) may be rewritten in terms of age-specific survival by replacing p^x by l_x . In practice, one usually estimates annual survival as a series of rates like p_0 = survival from recruitment through the first year, p_1 = survival in the second year, etc., and l_x is then obtained as the product of several such rates.

If reproduction is regarded as a continuous process (as was done in the original development of the equations), then it is necessary to replace the summations above by integral signs, and the geometric rate of increase, $(1+r)^x$, now becomes exponential. However, solutions require the use of the form involving summations, in any case. Hence, we will consider only the summation forms here. These are recapitulated below, using l_x instead of p^x :

$$\frac{1}{b} = \sum_{x=0}^{\infty} (1+r)^{-x} l_x \quad (11.22)$$

$$c_x = b(1+r)^{-x} l_x \quad (11.23)$$

$$1 = \sum_{x=0}^{\infty} (1+r)^{-x} l_x m_x \quad (11.24)$$

The rate, r , is widely known as the "intrinsic rate of increase" (a term coined by A. J. Lotka), and has been subjected to all sorts of attempts at definition in terms of optimal conditions, etc. The best definition is that of equation (11.24), i.e., given constant age-specific reproductive (m_x) and survival rates (l_x) a population will tend to develop a stable age structure, and, if that age structure is attained, the population then increases at rate r . From a practical point of view, one may doubt the likelihood that a particular population has or will actually attain the above conditions, but r is still useful as a quantity defined by equations (11.24) for a given observed set of rates m_x and l_x .

Before considering some simplifications of the above equations it is worth noting that a similar development can be constructed for males by assuming a 1:1 sex ratio at recruitment, and that p_1 represents male survival. Then:

Age structure for males:

$$c_x = \frac{q(1+r)}{1+r} (1+r)^{-x} p_1^x \quad (11.25)$$

$$\text{Total population at year } i = (1+r)^i \left[1 + \frac{q(1+r)}{1+r} \right] \quad (11.26)$$

and, the sex ratio in the population then is:

$$\text{females/males} = \frac{q1+r}{1+r} \quad (11.27)$$

11.15 Net rate of increase

Some variations of the basic equations (11.22 to 11.24) are useful. One is the "net rate of increase" or "net reproduction rate" defined as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (11.28)$$

or, in terms of an integral (continuous reproduction):

$$R_0 = \int_0^{\infty} l_x m_x dx \quad (11.29)$$

These equations correspond to equation (11.24) with $r=0$, whereupon $R_0=1$ and the population is "stationary" (neither increasing or decreasing). There is thus the expectation that if $R_0 > 1$ the population should be increasing and vice versa. This is true enough if the age structure is that given by equation (11.19), otherwise it is not necessarily the case, since the equations do not take current age-structure into account.

R_0 has also been used to define something called the "length of a generation". In those species reproducing only once, the length of a generation can be explicitly defined. Familiar examples are insects that reproduce annually and die (or the cicadas, with as much as 17 years of larval development before reproduction and death in a few weeks of adult life), and the Pacific salmon with 3 or 4 year "cycles" between spawning of parental and filial generations. But when a species exhibits repeated and age-specific reproduction the replacement of one generation by another is a gradual process, with no specific time of transition. Thus there is a need to define some measurement if one wants to consider "length of a generation." The necessity for a definition is of major importance in terms of genetic behavior of a population.

Leslie (1966) gives several definitions of length of a generation, with his own recommendation being:

$$\bar{T} = \int_0^{\infty} x e^{-rx} l_x m_x dx \quad (11.30)$$

Leslie pointed out that this is not the same as an earlier definition:

$$T = \frac{\log_e R_0}{r} \quad (11.31)$$

Another definition that has been used is that of the mean age of mothers at the birth of their daughters or "cohort generation time":

$$T_c = \frac{\int_0^{\infty} x l_x m_x dx}{R_0} = \frac{\int_0^{\infty} x l_x m_x dx}{\int_0^{\infty} l_x m_x dx} \quad (11.32)$$

which is equivalent to T when $r=0$. The above equations are written with integrals as would be the case for continuous reproduction, but summation signs need to be substituted for cases where reproduction occurs at discrete time intervals.

Equation (11.31) seems difficult to justify as a useful measurement of "generation time," and for most practical purposes one might elect to use either equation (11.30) or (11.32), with the latter being a little less trouble to calculate. However, students should consult Leslie's paper and Caswell (1989, 2001) if they have occasion to use mean length of a generation.

11.16 Practical applications

With a few exceptions, the actual use of equations (11.22) to (11.24) entails circumstances that permit various simplifications. The exceptions consist largely of human populations (demographic and actuarial data) and a few species that have been extensively studied in the laboratory or in domestication. The main simplification results from the observation that 2 or 3 different survival rate estimates may serve to represent l_x . This largely results as a consequence of constant survival rates for mature individuals. Since most wild animals die violently from predation, accidents, or hunting, and do so at rates great enough to preclude more than a small fraction reaching any sort of old age, it is difficult to determine whether adult age-classes may exhibit age-specific mortality which is simply not observed or whether the adult survival rate is indeed virtually constant. Since very large samples are needed to demonstrate relatively small changes in survival rate, and since year-to-year changes in overall rates do clearly occur, it is not surprising that age-specific rates have seldom been recorded for mature animals.

Whether the younger age-groups are assigned one or two survival rates depends in part on longevity of the species and on quality and quantity of the available data. In most circumstances it seems desirable to use two rates; one for an interval including birth and the relatively short period of high mortality just after birth, and the second for the subsequent interval up to maturity. Very likely early adult life should also be characterized by an additional rate, but only rarely are sufficient data available to do so. The choice of number of survival rates also depends on the choice of age for recruitment to the population being studied. Thus if new recruits are not tallied until they are nearly mature, two survival rates may suffice.

Somewhat similar considerations may apply to reproductive rates. Many avian species appear to have a virtually constant clutch size, so that only one reproductive rate need be used, while the shorter lived mammals may have a smaller first litter, but effectively constant litter size thereafter. Many of the larger mammals show distinct age-specific rates, increasing to the "prime of life", holding relatively constant for some considerable time thereafter, and possibly declining to nearly zero in "old age". In practice, then, age-specific reproductive rates may constitute from two values (zero for younger age-classes and a constant rate for all mature age classes) to perhaps 3 to 5 significantly different rates.

Given a reduced set of l_x and m_x values as suggested in the above paragraphs, one can then simplify the calculations required by equations (11.22) to (11.24) or produce alternative versions to serve as the basis of inferences about population trend, or allowable harvest, etc. Leslie (ibid.) gives an example for a seabird (Uria aalge, the guillemot or murre) which serves to illustrate the procedure. This species first breeds at 3 years of age and it is assumed that clutch size remains constant thereafter. Leslie calculated m_x on the basis of the number of young at fledgling stage, "ready to go to sea", and equal numbers of males and females, so that we start dating events at this time, with $m_0=0$, $m_1=0$, $m_2=0$, $m_3=F=m_x$ ($x \geq 3$), where F is a constant (since only a single egg is hatched by a breeding pair, F is at most 0.5). Survival for the first year after hatching was defined as P_0 , while that in the second year was P_1 , and the rate in all subsequent years was considered a constant value, P . The essential rates are thus:

Age (x)	0	1	2	3	$x(x \geq 3)$
Survival	1	P_0	P_1	P	P
l_x	1	P_0	$P_0 P_1$	$P_0 P_1 P$	$P_0 P_1 P^{x-2}$
m_x	0	0	0	F	F

If we let $\lambda = 1+r$, as used by Leslie, then equation (11.15) becomes:

$$\begin{aligned}
 1 &= \lambda^{-0}(1)(0) + \lambda^{-1}P_0(0) + \lambda^{-2}P_0P_1(0) + \lambda^{-3}P_0P_1PF + \lambda^{-4}P_0P_1P^2F \\
 &= \lambda^{-3}P_0P_1F(1 + \lambda^{-1}P + (\lambda^{-1}P)^2 + \dots) \\
 &= \lambda^{-3}P_0P_1F(1 - \lambda^{-1}P)^{-1}
 \end{aligned}$$

so that:

$$1 - \frac{P}{\lambda} = \lambda^{-3}P_0 P_1 F$$

and:

$$\lambda^3 - P\lambda^2 - P_0P_1PF = 0 \quad (11.33)$$

Hence, given values for P_0 , P_1 , P , and F , one can calculate λ (and thus r) by solving the cubic equation (11.33).

The net rate of increase, R_0 is (equation 11.28):

$$R_0 = p_0 p_1 F (1 + p + p^2 + \dots) = \frac{p_0 p_1 p F}{1 - p} \quad (11.34)$$

so that if $r=0$ (and thus $\lambda=1$) equations (11.33) and (11.34) are identical and represent conditions when the population is of constant size. Thus one can consider the plausibility of the available estimates of P_0 , P_1 , P and F over long periods of time, or conjecture as to the future of the population if survival and/or reproductive rates change.

Using equation (11.24) and $\lambda = 1+r$, we calculate:

$$\begin{aligned} \frac{1}{b} &= 1 + \lambda^{-1} p_0 + \lambda^{-2} p_0 p_1 + \lambda^{-3} p_0 p_1 p + \dots \\ &= 1 + \lambda^{-1} p_0 + \lambda^{-2} p_0 p_1 + \lambda^{-3} p_0 p_1 p (1 - \lambda^{-1} p)^{-1} \end{aligned}$$

which provides an estimate of b from which the stable age-structure can be obtained with equation (11.23). Again, if $r=0$, then $\lambda=1$, simplifying the equation somewhat.

Introducing additional age-specific reproductive rates poses no special problems, beyond including the necessary quantities in a table like the one used above, and keeping track of the necessary algebraic results. This gives results like eq. (11.11). Sometimes, as was done by Leslie in his study, it is convenient to use all adults (3 years old and older in this case) as a base, and calculate proportions of nestlings, 1 and 2 year-olds relative to that base. In practice, one may often not be able to determine the exact age of an "adult", necessitating such an arrangement.

11.17 Exercises

11.17.1 Discrete and continuous rates of increase

Most species show some degree of seasonality in reproduction. There is thus an annual cycle of numbers, peaking at the period of maximum reproductive effort, and reaching a minimum when reproduction is at the lowest annual rate (or not occurring at all in many species). Annual rates of growth should thus be computed from measurements made at the same time each year, and the "compound interest" formula is the appropriate model for population growth:

$$N_{t+1} = N_t (1 + r)^t$$

where t is expressed in years. There are some species that will reproduce continuously under suitable conditions. The continuous time model:

$$N_{t+1} = N_t e^{rt}$$

then provides a close approximation to observations, and t can be measured in time units of varying length.

As a matter of mathematical convenience and custom, many authors use the continuous model exclusively. When r is small, and t not too large, it makes little difference which model is used. Students should try values of $r = 0.01, 0.05, 0.10$ for $t = 5, 10, 20$ in the two equations in order to see how the results differ.

If we utilize λ in equations, it can represent either case, i.e., $\lambda = e^r$ or $\lambda = 1+r$. The main difference arises when one reports a rate of increase as r . In one case $r = \log_e \lambda$, and in the other, $r = \lambda - 1$. Students should try calculating r from values of λ calculated from the two definitions (i.e., suppose $\lambda = 1.25$, and calculate $r = \log_e \lambda$ and $r = \lambda - 1$ and compare the results. Compare the series expansions of $\log_e(1+r)$ and e^r for further understanding.

11.17.2 Constructing a stable age distribution

Make a numerical version of the table of Sec. 11.13 using $p=0.9$ and $r=0.1$. Carry it to the fifth generation. Note that each succeeding entry for a given year class is simply p times the previous value, and the last year class in each generation is given by the last term in the equation for total population size given below the table. Check to be sure that your values add to $(1+r)^i$ for the i^{th} generation. Convert the last row into proportions, and calculate the stable age distribution from eq. (11.23) and enter it as a final row in the table. Note that the final year class in each row represents newborns and is consequently c_0 , so that you enter the stable age entries from right to left in the last row.

Since survivors from the zeroth generation are calculated as p^i , it will take quite a long time before that generation is reduced to a level commensurate with the result expected from eq.(11.15). In 20 years, we have $(0.9)^{20} = 0.1216$. Compare this with the result you get from eq. (11.23). Hence, with high survival rates, changes in age structure can persist for fairly long time periods.

11.7,3 Calculating rate of increase for fur seals.

Use of equations (11.22) to (11.24) can be illustrated with data on the northern fur seal (*Callorhinus ursinus*). The data appear in Table 11.17.1 below and consist of age-specific reproductive rates (m_x) and annual survival rates (p_x , which are often written as s_x). The m_x entries in the table are one-half of pregnancy rates observed in extensive pelagic collections of fur seals (some 12,000 seals were aged). Survival rates were estimated in various ways. Survival from birth to age 3 comes from estimating pup numbers and the number of 3 year-old males present at the time they were harvested for furs. This three year rate was arbitrarily partitioned over the first 3 years of life. A single adult survival rate was estimated from the rate of decrease of the relative size of age classes from age 3 up to age 16, and then from averaging ratios of pairs of year-classes for animals older than age 16. More details are available in Eberhardt (1981).

Calculations proceed by forming an l_x column from the annual survival rates simply by taking products, with $l_0 = 1$ by definition. Since $m_x = 0$ for the early age-classes, equation (11.20) can be written as:

$$1 = \sum_{x=3}^{24} \lambda^{-x} l_x m_x$$

The equation is solved for λ by iteration, i.e., one chooses a value of λ in the neighborhood of unity, calculates the sum, and either increases or decreases λ according as the sum exceeds or is less than unity, continuing until the sum is sufficiently close to unity. Programming a calculator or computer to do the work is desirable if one has more than a few such calculations to carry out.

One iterative method uses linear interpolation. From the data of Table 11.15.1, we can compute that the sum of the $l_x m_x$ is 1.0604. This is equivalent to setting $\lambda = 1.0$. Evidently λ is somewhat larger than unity, so we might try $\lambda = 1.01$. This gives a sum of 0.95787. A simple way to remember the interpolation process is just to note that the two pairs of points computed thus far determine a straight line, $y = a + bx$. It is convenient to let $y = \lambda$, and x represent the sum calculated from the equation above, since we want to predict what value of y results from $x=1.0$. The slope (b) is the rate of change in y resulting from a change in x from 1.0604 to 0.95785. This gives:

$$b = \frac{1.00-1.01}{1.0604-0.95787} = -0.0975324.$$

The intercept, a , is then:

$$a = y - bx = 1.01 + 0.0975324(0.95787) = 1.10342,$$

so the line is thus:

$$y = 1.10342 - 0.0975324x$$

Setting $x=1$ gives $\lambda=1.00587$. Using this value in eq. (11.20) gives a sum of 0.999006. Another iteration can be obtained by following the same procedure, using the new value and that for $\lambda=1$. This gives

$$y=1.10319 - 0.0956119x$$

or $\lambda=1.00578$ which yields a sum of 0.99992. A sketch is always helpful in keeping track of things in the interpolation process.

Linear interpolation formulas given in textbooks and manuals require fewer calculations, but the above procedure should be easy to remember. Other approaches can be used when a calculator or computer is programmed. Perhaps the simplest is to start with $\lambda=1$ and change it by some small increment which is positive or negative depending on whether the resulting sum (eq.(11.20) is greater or less than 1.0. As the sum decreases, then the increment should be made smaller, down to the order of accuracy wanted. As has been noted before here, one can conveniently avoid most of the above by using SOLVER in EXCEL.

When λ has been calculated, eq.(11.22) can be used to calculate the "birth rate per capita" (b) and eq.(11.23) then provides the proportions in various age-classes found in a population having the stable age structure. These are shown for the fur seal data in Table 11.15.1. Note that b is also the first entry in the age structure table (why?).

11.17.4 Rates of increase from Leslie's model

Leslie (1966) gave estimates of $p_0 = 0.7$, $p_1 = 0.8$, $p_2 = 0.9$ and $F = 0.2307$ for a guillemot (murre) population. Solving eq. (11.33) with these values requires finding the positive root of a cubic equation:

$$x^3 - 0.9x^2 - 0.116273 = 0$$

which has the solution $x = 1.01325$ ($=\lambda$). From eq. (11.28), we get $R_0 = 0.116273/0.1 = 1.1627$. Leslie also used $F = 0.375$ and $F = 0.50$ for illustrative purposes. Calculate λ and R_0 corresponding to these two values of F .

11.17.5 Calculating a stable age distribution for Leslie's data

For $F = 0.2307$ and the survival rates given in the exercise above, calculate the stable age distribution for Leslie's guillemots at the time of hatching, assuming that there are 1,000 adults (3 years of age and older). Use the equation following (11.24) to estimate b , and eq.(11.23) to obtain c_x .

11.17.6 Extending Leslie's simplified model

Leslie (1966) assumed that the guillemots began reproduction at age 3. As discussed in Sec. 11.15, he then produced a cubic equation, and solved that for λ . Often, one will not have the data to solve the resulting polynomial, but it may nonetheless be useful to explore possibilities with the data that are on hand. Thus Eberhardt and Siniff (1977) wrote the corresponding equation as:

$$1 = \lambda^{-a} p_0 p_1 p^a - 2F(1 - p\lambda^{-1})^{-1}$$

where a = age of first reproduction. Students should check to see that this reduces to eq. (11.33) when $a = 3$.

The quantity often missing in field studies is survival from birth to adulthood, so the above equation was rearranged by defining the ratio:

$$K = \frac{p_0 p_1}{p^2}$$

which is the ratio of juvenile survival to that of adults. This then gives:

$$K = \frac{\lambda^a - 1}{F p^a}$$

If we have estimates of F and p , it is then possible to explore the rates of increase likely to result from various ratios of juvenile to adult survival. Eberhardt and Siniff (1977:Fig. 3) plotted some values for convenient inspection of possibilities. Other arrangements of the simplified equations were used to examine other facets of marine mammal population dynamics. An important conclusion was that the age of first reproduction is not as important in determining rates of increase as seems to be assumed in many references.

11.17.7 Calculating length of a generation

Try the equation of Sec. 11.14 on the guillemot data given above. You will need to replace integrals by summations and use sums of series. Make a table showing the three estimates for length of generation for each of the three values of F given in the example.

Table 11.17.1. Age structure data for northern fur seals.

Age	c_x	m_x	l_x	p_x
0	0.18876	0	1	1
1	0.10288	0	0.548	0.548
2	0.08183	0	0.4386	0.800
3	0.07419	0.0015	0.400	0.912
4	0.06727	0.0205	0.3648	0.912
5	0.06100	0.192	0.3327	0.912
6	0.05531	0.3815	0.3034	0.912
7	0.05015	0.4020	0.2767	0.912
8	0.04547	0.433	0.2523	0.912
9	0.04123	0.4495	0.2301	0.912
10	0.03738	0.4405	0.2099	0.912
11	0.03390	0.446	0.1914	0.912
12	0.03074	0.440	0.1746	0.912
13	0.02787	0.434	0.1592	0.912
14	0.02527	0.420	0.1452	0.912
15	0.02291	0.4135	0.1324	0.912
16	0.02077	0.402	0.1207	0.912
17	0.01396	0.341	0.0816	0.676
18	0.00893	0.3325	0.0525	0.643
19	0.00499	0.273	0.0295	0.562
20	0.00310	0.239	0.0185	0.626
21	0.00135	0.293	0.0081	0.438
22	0.00054	0.178	0.0032	0.4
23	0.00016	0.05	0.0009	0.3
24	0.00003	0	0.00019	0.2

Exercise 11.17.8. **The Leslie matrix.**

The results given in this Chapter depend on the discrete form of Lotka's equation and the assumption of a birth-pulse population as expressed in eqs. (11.5) and (11.6). Because the Leslie matrix is widely used, students should be familiar with it. The following table gives the elk data of Table 11.1 expressed as a Leslie matrix (but the matrix is printed in two blocks because of space constraints, and the row and column numbers are not part of the matrix).

[illegible]

14	0	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0

	11	12	13	14	15	16	17	18	19	20	21	22	23
0.3097	0.3049	0.2979	0.2876	0.2730	0.2527	0.2251	0.1895	0.1466	0.1001	0.0567	0.0243	0.0243	
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.9795	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0.9719	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0.9608	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0.9445	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0.9208	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0.8865	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0.8377	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0.77	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0.6791	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0.5632	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0.4261	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0.2813	0	0

The first row of the matrix contains the reproductive values for ages listed in the column headings (these are ages one and older as newborns do not appear in the Leslie matrix). The reproductive rates are those of the first column of Table 11.1 multiplied by survival from birth to age 1 (0.6745). The entries in the diagonal starting with age 2 (left column of numbers) are survival rates from age one onwards as shown in Table 11.1. A stable age distribution is calculated as in eq.(11.6) except that one has to recode the age-classes so that age one is now coded as age-class zero. This lets us set up a stable age distribution for 10,000 elk which is used as an age vector (column of ages) along with the MMULT function of EXCEL. To use that function, one enters the range of the Leslie matrix followed by a comma and the range of the initial age structure vector (must have the same number of rows as the Leslie matrix). The MMULT function then produces a new vector which is the population structure one year later. Because we started out with the stable age structure, the same proportions are obtained as in the initial age structure. If one starts with a

different age structure, then repeated projections show a convergence to the stable age structure. The several computations are as follows:

		lambda	1.20133									
SURVIVAL			Calc. for		COHORT		1st	2nd	3rd			
RATES	l(x)		C(x)	c(x)			project	prop	proj	prop	proj	prop
0	0.995	1	1	0.1798	1798.2	2160.3	0.1798	2595.3	0.1798	3117.8	0.180	
1	0.995	0.995	0.828	0.149	1489.4	1789.2	0.149	2149.5	0.149	2582.3	0.149	
2	0.9934	0.990	0.686	0.123	1233.6	1481.9	0.123	1780.3	0.123	2138.8	0.123	
3	0.994	0.983	0.567	0.102	1020.1	1225.4	0.102	1472.1	0.102	1768.5	0.102	
4	0.9936	0.978	0.469	0.084	844.0	1013.9	0.084	1218.1	0.084	1463.3	0.084	
5	0.9929	0.971	0.388	0.070	698.1	838.6	0.070	1007.4	0.070	1210.3	0.070	
6	0.9918	0.964	0.321	0.058	577.0	693.1	0.058	832.7	0.058	1000.3	0.058	
7	0.9903	0.957	0.265	0.048	476.3	572.2	0.048	687.4	0.048	825.8	0.048	
8	0.988	0.947	0.218	0.039	392.7	471.7	0.039	566.7	0.039	680.8	0.039	
9	0.9845	0.936	0.180	0.032	322.9	387.9	0.032	466.0	0.032	559.9	0.032	
10	0.9795	0.921	0.147	0.026	264.6	317.9	0.026	381.9	0.026	458.8	0.026	
11	0.9719	0.902	0.120	0.022	215.8	259.2	0.022	311.4	0.022	374.1	0.022	
12	0.9608	0.877	0.097	0.017	174.6	209.7	0.017	251.9	0.017	302.7	0.017	
13	0.9445	0.843	0.078	0.014	139.6	167.7	0.014	201.5	0.014	242.1	0.014	
14	0.9208	0.796	0.061	0.011	109.8	131.9	0.011	158.4	0.011	190.3	0.011	
15	0.8865	0.733	0.047	0.008	84.1	101.1	0.008	121.4	0.008	145.9	0.008	
16	0.8377	0.650	0.035	0.006	62.1	74.6	0.006	89.6	0.006	107.6	0.006	
17	0.77	0.544	0.024	0.004	43.3	52.0	0.004	62.5	0.004	75.1	0.004	
18	0.6791	0.419	0.015	0.003	27.7	33.3	0.003	40.0	0.003	48.1	0.003	
19	0.5632	0.285	0.009	0.002	15.7	18.8	0.002	22.6	0.002	27.2	0.002	
20	0.4261	0.160	0.004	0.001	7.4	8.8	0.001	10.6	0.001	12.7	0.001	
21	0.2813	0.068	0.001	0.000	2.6	3.1	0.000	3.8	0.000	4.5	0.000	
22		0.019	0.000	0.000	0.6	0.7	0.000	0.9	0.000	1.1	0.000	
sum			5.561	1.000	10000	12013	1.000	14432	1.000	17338	1.000	
B=			0.1798									

Repeat the calculations in order to become familiar with the Leslie matrix. There are many more manipulations possible, and one can calculate lambda directly from the matrix, and so on.

Exercise 11.17.9 Convergence to stable age structure.

The above exercise started out with a stable age structure. Use the same matrix for projections, but start the projections with a different initial age vector. Enter 4287 above the first column of the spreadsheet that will contain your calculations, number a column from 1 to 23 as in the above exercise, but now make the "cohort" entries by multiplying by 0.7 raised to the power of the row numbers, i.e., entries will be calculated from $4287 \cdot 0.7^x$, where x is the row number (1 to 23). The first cohort should be as shown below. Now project out 10 years proceeding as in the previous exercise, and note that the proportions in each age class approach the stable age distribution as in the previous exercise.

	4287
	0.7
COHORT	
1	3000.90
2	2100.63
3	1470.44
4	1029.31
5	720.52
6	504.36
7	353.05
8	247.14
9	173.00
10	121.10
11	84.77
12	59.34
13	41.54
14	29.08
15	20.35
16	14.25
17	9.97
18	6.98
19	4.89
20	3.42
21	2.39
22	1.68
23	1.17
SUM	10000.26